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The differences in carbon dynamics between boreal dwarf shrubs and Scots pine seedlings in a microcosm study

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Abstract

Aims

The ground level of boreal pine forests consists of a dense layer of ericaceous shrubs, herbs, grasses, mosses and lichens. The primary productivity of this forest floor vegetation is notable but the role the most common ericoid dwarf shrub plant species, *Calluna vulgaris*, *Vaccinium myrtillus* and *Vaccinium vitis-idaea*, play in carbon (C) cycling in these ecosystems is poorly understood. Here, we studied their C dynamics in detail using plants of similar size (age 14–19 months) in a microcosm study.

Methods

We determined the full C balances of these dwarf shrubs for the first time and compared them to those of *Pinus sylvestris* by using long-term biomass accumulation, ^{13}C pulse labelling and CO_2 exchange measurements in a controlled laboratory experiment.

Important Findings

Pinus sylvestris had significantly higher biomass-based C fluxes than dwarf shrubs, both aboveground and belowground, but the dwarf shrubs did not differ in the biomass-based fluxes. We showed that root respiration of the evergreen ericoid dwarf shrubs was sensitive to the aboveground light conditions as belowground respiration was 50–70% higher under light compared with dark conditions. Such light-related differences were not observed for Scots pine. The observed differences in C dynamics are important in estimating the origin of belowground CO_2 fluxes and in evaluating their biological relevance. Our results improve current understanding of CO_2 sources and sinks in boreal ecosystems.

Keywords: photosynthesis, autotrophic respiration, NPP, ^{13}C labelling

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INTRODUCTION

The ground layer of boreal pine forests is vegetated and therefore photosynthetically active, unlike in many other forest ecosystems. A dense community of plant species consisting of ericaceous shrubs, herbs, grasses, mosses and lichens colonizes the ground of boreal pine forest ecosystems. They affect the ecosystem and soil functioning in several ways, for example physically by providing a buffer between air and soil affecting soil temperature and moisture which are crucial factors in many belowground processes (Adamczyk *et al.* 2016; Nilsson and Wardle 2005; Wardle *et al.* 2003; Wardle and Zackrisson 2005). In addition, the ground vegetation of boreal forests also makes important contributions to the cycling of essential nutrients like nitrogen (DeLuca *et al.* 2002; Näsholm *et al.* 1998).

The primary productivity of this ground vegetation is notable (Goulden and Crill 1997; Kolari *et al.* 2006; Kulmala 2011; Moren and Lindroth 2000). The share of ground vegetation contributing to CO_2 uptake of a forest ecosystem naturally depends on site and vegetation characteristics but it has been reported varying momentarily between 3% and 50% (Goulden and Crill 1997; Subke and Tenhunen 2004). Most common annual estimates lay between 10% and 20% (Bergeron *et al.* 2009; Ilvesniemi *et al.* 2009; Kolari *et al.* 2006; Kulmala *et al.* 2011; Swanson and Flanagan 2001).

A large proportion of the soil CO_2 emissions originates from root exudates containing carbohydrates that are

rapidly metabolized by microorganisms (Högberg *et al.* 2001; Pumpanen *et al.* 2009). These microorganisms are involved in the decomposition of organic substances in soil due to the so called priming effect (Kuzyakov *et al.* 2000). Belowground carbon (C) allocation is mainly studied using canopy layer plant species. However, it is evident that also dwarf shrubs in the ground layer allocate C belowground to microorganisms associated to their roots including symbiotic mycorrhiza and bacteria (Smith and Read 2008).

As listed above, there is a variety of estimates for the primary production of ground vegetation in boreal forests. However, it is still unclear how much of this primary productivity is truly allocated to long-lived structural compounds or if it is briefly stored and released via root exudates and autotrophic respiration. The carbon balance of ground vegetation plant species is poorly identified and it is not known which part of the observed CO_2 emissions by soil chambers or the eddy covariance (EC) technique actually originates from the ground vegetation and which fraction originates from trees and the decomposition of soil organic matter. The partitioning of EC-derived net ecosystem exchange into respiration and gross primary production was recently shown to be uncertain (Wehr *et al.* 2016). Therefore, additional information on the species-specific carbon balance, i.e. biomass accumulation and rates of belowground and aboveground respiration, is needed to improve our understanding of the carbon fluxes inside a boreal forest ecosystem.

The aim of this study was to improve the reliability of Scots pine boreal forest carbon balance estimates by quantifying the primary production of the most common species on the forest floor and reveal their C allocation patterns using biomass analysis (long-term allocation), ^{13}C-labelling (short-term allocation) and CO_2 exchange measurements (photosynthesis and respiration). As a tool, we used microcosms as Pumpanen *et al.* (2009) who studied the carbon dynamics of common tree seedlings but did not consider the dwarf shrubs.

MATERIALS AND METHODS

The plant material

The seedlings of *Vaccinium vitis-idaea* L. (Vacvit), *Vaccinium myrtillus* L. (Vacmyr) and *Calluna vulgaris* (L.) Hull (Calvul) were propagated from seeds originating from southern Finland. The berries of Vacvit and Vacmyr were picked in late summer 2011 and stored in freezer (−18°C) for 9 months. The berries were melted in room temperature for 3 h before washing. The seeds were separated from pulp and dried in room temperature. For *Pinus sylvestris* L. (Pinsyl), we used seed lot M29-92-0059 Sv. 318 Ullanristi, whereas the seedlings of Calvul were germinated naturally from sieved humus. The *Vaccinium* species were germinated and grown for 9 months and Pinsyl for 3 months in sterile test tubes (Heinonsalo *et al.* 2015) before planting 14 seedlings of each species in humus-filled microcosms (Pumpanen *et al.* 2009). The soil volume of one microcosms was ~178 cm^3 and was filled with homogenized humus collected from a Scots pine dominated stand near Hyytiälä Forestry Field Station, southern Finland. In addition, 14 microcosms lacking seedlings were established as control treatments.

The seedlings in the microcosms grew in a growth chamber with a stable temperature (18/14°C day/night), stable PAR intensity (170 µmol m^{-2} s^{-1}) and with a day length of 18 h for 9 months. The microcosms were regularly watered. The experimental conditions used during germination are reported in detail by Adamczyk *et al.* (2016).

Roots and rhizomes were gently removed from soil and washed from any adhering soil particles after the experimental treatment (see later). Rhizomes were growing nearly laterally without fine roots looking morphologically very different from roots. Thus, those were easy to separate. The plant material was lyophilized with a Christ Gamma 2–16 LSC Freeze dryer (SciQuip Ltd, Merrington, UK) for 3 days. The samples were then separated into organs (stem, leaves, rhizome, roots), weighted and ground into a fine powder for stable isotope sampling (see later) with a mechanical grinder (2000–230 Geno/Grinder, Spex SamplePred, USA). Total biomass was treated as daily growth (mg d^{-1}) to allow the comparison of seedlings with the slightly different growth periods. Differences in growth rates and in the biomass of different organs of the species were compared using an one-way analysis of variance (ANOVA) and Tukey honest significant difference (HSD) test in *R* (version 3.0.2, R Core Team, 2014) after an arcsine square root transformation. The shares of aboveground and belowground biomasses were tested without any transformation. The normality of the data sets was verified using the Shapiro–Wilk test (*R*).

CO_2 and H_2O exchange

Eight seedlings from each species and 12 controls treatments lacking a seedling were selected for gas exchange measurements. The CO_2 and H_2O exchange rates of the shoots and belowground parts were measured by enclosing them in separate, airtight compartment chambers (see for details Pumpanen *et al.* 2009). First, we enclosed the seedling in darkness and measured the CO_2 emissions of the belowground parts. To keep the air pressure unaltered, synthetic compensation air with controlled CO_2 and H_2O concentrations was introduced in the chamber at 0.5 l min^{-1} flow while the concentrations of the outflow was analysed using a Licor LI-840 a Licor LI-7000 (Li-Cor Inc., Lincoln, Nebraska). We continued to measure the flux for ~1.5 h controlling the temperature to 25°C with a cooling system circulating cold water around chambers. Then, we measured CO_2 and H_2O concentration of the aboveground compartment chamber outflow similarly. After measuring the belowground and aboveground fluxes of four darkened plants, we repeated the same measurements but this time placed a light source (PAR = 120 µmol m^{-2} s^{-1}) in front of the plant. The experimental setup used to measure gas exchange rates in these microcosms is described in detail by Pumpanen *et al.* (2009) that used the same setup when

comparing the carbon allocation between common boreal tree species.

Gas exchange rates of the different species in the aboveground and belowground compartments in light and dark conditions were separately calculated from the difference in gas concentration between the outflow and the reference channel with known air flow (Pumpanen *et al.* 2009). The fluxes were relatively stable after 1.5 h but to be exact, we fitted a saturating Michaels–Menten type equation over the CO_2 fluxes during the 1.5 h to determine the steady state, F (μmol s^{-1}), as follows:

$$f(t) = \frac{F\ t}{\alpha + t} \quad (1)$$

In the equation, $f(t)$ is the measured CO_2 flux (μmol s^{-1}) at moment t whereas F (μmol s^{-1}) and α (s) are fitted parameters. The parameters were estimated using 'nsl' function in *R*. Obtained F values were used as the CO_2 fluxes in the further analyses. Insufficient stabilizing of the flux was detected from two samples i.e. f (1.5 h) differed greatly from F. These were a belowground measurement of a Pinsyl in light and dark and a belowground measurement of a Vacmyr in the dark. This indicated potential gaseous leakage in the experimental chamber and these fluxes were eliminated from further analysis.

All measured CO_2 fluxes are summarized in the Fig. 1. The respiration aboveground (R_{above}) and net exchange (NE_{above}) were determined as the F values derived from the aboveground compartment in darkness and in light, respectively. R_{above} was always positive indicating respiratory emissions, whereas NE_{above} was negative since the rate of photosynthetic uptake of CO_2 exceeded the rate of respiratory emissions. Assuming that R_{above} is same in light and darkness, rate of photosynthesis (P) can be calculated as the difference between R_{above} and NE_{above}:

$$P = R_{above} - NE_{above} \quad (2)$$

The CO_2 emissions from the humus (R_{humus}) were determined as the mean F in the control microcosms that did not contain a seedling. Root respiration (R_{root}^{light} and R_{root}^{dark}) was calculated as the difference between the F value in the belowground compartment (R_{below}^{light} and R_{below}^{light}) and R_{humus} both in light and in dark conditions:

$$R_{root}^{light} = R_{below}^{light} - R_{humus} \quad (3)$$

$$R_{root}^{dark} = R_{below}^{dark} - R_{humus} \quad (4)$$

Total respiration (R_{tot}) was calculated as the sum of R_{above} and R_{root}, where R_{root} was determined as an average of R_{root}^{light} and R_{root}^{dark} where possible negative values were replaced by the species-specific mean of available measurements:

$$R_{tot} = \frac{1}{2}\left(R_{root}^{light} + R_{root}^{dark}\right) + R_{above} \quad (5)$$

All fluxes were normalized by dividing them by either total mass or leaf mass. Net primary production (NPP) was calculated as the difference between P and R_{tot}.

Rate of transpiration (T, mmol s^{-1}) was calculated as the H_2O emission from the aboveground compartment in light. Water use efficiency (WUE) was calculated from the rates of photosynthesis and transpiration, as follows,

$$WUE = \frac{P}{T} \quad (6)$$

The differences between the species in the normalized fluxes were tested using an one-way ANOVA and the Tukey HSD test

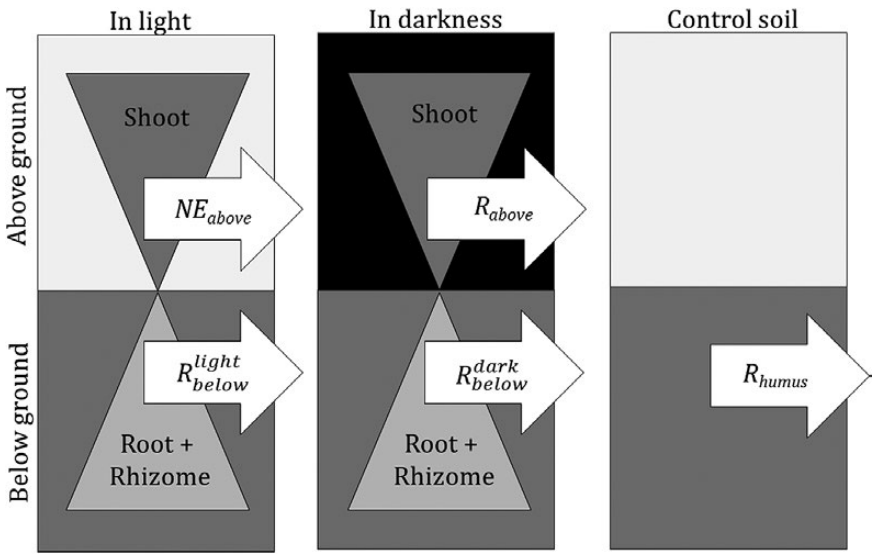

Figure 1: summary of the measured CO_2 fluxes.

in *R* after verifying the normality of the data sets by Shapiro–Wilk test (*R*). The differences between root respiration in light and dark conditions were tested with paired *t*-test in *R*.

Stable isotope labelling

Stable isotope labelling took place after the gas exchange measurements. The seedlings were grown in a constant light environment and exposed to ^{13}C for 2 h per day over a 5-day period. 1.5 ml of 100% $^{13}CO_2$ was injected into a 1000 ml shoot cuvette made of Perspex ® glass and the cuvette was made airtight for the incubation. Eight individuals per species were labelled whereas six per species acted as unlabeled controls. We used a standard harvesting protocol where all plants were harvested 3 to 4 days after the last labelling event. We chose the timing according to Pumpanen *et al.* (2009) who found in a similar microcosms experiment that the label in Scots pines seedlings started to show up in the root and rhizosphere respiration after 12 h remaining high until 1 week following the labelling.

A subsample of each organ was sent to UC Davis Stable Isotope Facility (Davis, CA, USA) for ^{13}C analysis. ^{13}C levels were measured by an Elementar Vario EL Cube or Micro Cube elemental analyzer (Elementar Analysensysteme GmbH, Hanau, Germany) interfaced to a PDZ Europa 20-20 isotope ratio mass spectrometer (Sercon Ltd., Cheshire, UK). This analysis also provided C and N quantities. In order to study short-term allocation of the assimilated carbon, we derived the relative distribution of the ^{13}C label by first deriving the mean of the signatures ($\overline{\delta}_s^x$) in each unlabeled organ (*x*) of the species *s* and then deriving the individual differences between labelled signatures and the unlabeled mean ($d_s^x = \delta_s^x - \overline{\delta}_s^x$). We used the absolute δ_s^x values in this estimate. Then, we calculated the mean share of the label in different organs of a plant by deriving each difference by the sum of differences of that individual ($d_s^x / \sum d_s^x$). The proportions were tested using an one-way ANOVA and the Tukey HSD test in *R* after an arcsine square root transformation.

RESULTS

Plant growth rates and biomass allocation

The biomass growth rates of Calvul and Vacmyr were significantly different from each other with Calvul exhibiting the highest growth rate while Vacmyr exhibited the lowest growth rates (Table 1). The biomass allocation was similar between the species (Table 1, see online supplementary Fig. S1) except for Vacmyr that has annual leaves unlike the other species. Vacmyr allocated 21% of the biomass to the leaves and 31% to the stems, whereas those of the other species were 42–52% and 13%, respectively. Calvul had the highest aboveground share (66%) but that of Pinsyl (60%) did not differ significantly. *Vaccinium* are the only species with rhizomes included in this study. Vacvit and Vacmyr allocated 15% and 6% of their biomass to the rhizome, respectively. The share of roots did not differ between the species, although the rhizome increased the belowground share of Vacmyr and Vacvit.

The carbon content of the organs was ~49% (see online supplementary Table S1) without any significant differences between the species. The C/N ratios of the organs differed significantly between the measured species being overall the highest in Calvul and lowest in Pinsyl (see online supplementary Table S2).

CO_2 exchange and transpiration

Pinsyl had the highest rate of photosynthesis (nmol g^{-1} s^{-1}). Aboveground and belowground respiration and transpiration differed significantly from those of dwarf shrubs when normalized by total biomass (Table 2). Vacmyr, which has annual leaves, had similar NE_{above}, P, R_{tot} and T compared to Pinsyl but differed significantly from those of Vacvit and Calvul when normalized by leaf mass only (see online supplementary Table S3). The NPP values were similar between the species (Table 2). The mean R_{humus} per dry mass was 0.317 µmol kg^{-1} s^{-1}.

Table 1: the number of samples (N) and the growth rates (mg d^{-1}) of total biomass and specific fractions ± standard error of the measured species

Species	Calvul	Pinsyl	Vacmyr	Vacvit
N	14	14	14	12
Total	8.08 ± 3.03	6.02 ± 2.29	5.44 ± 2.04	6.57 ± 1.92
Above ground	5.31 ± 2.10 (66)a	3.60 ± 1.48 (60)ab	2.85 ± 1.28 (52)c	3.62 ± 1.20 (55)bc
Below ground	2.77 ± 1.25 (34)a	2.42 ± 0.91 (40)ab	2.60 ± 0.91 (48)c	2.95 ± 1.21 (45)bc
Stem	1.08 ± 0.54 (13)a	0.76 ± 0.28 (13)a	1.69 ± 0.69 (31)b	0.86 ± 0.28 (13)a
Leaves	4.23 ± 1.70 (52)a	2.84 ± 1.23 (47)ab	1.16 ± 0.63 (21)c	2.76 ± 0.98 (42)b
Roots	2.77 ± 1.25 (34)ab	2.42 ± 0.91 (40)a	2.24 ± 0.89 (41)a	2.00 ± 1.09 (30)b
Rhizome	0.00 ± 0.00 (0)a	0.00 ± 0.00 (0)a	0.35 ± 0.23 (6)b	0.95 ± 0.45 (15)c

The percentage of the organ in the total biomass (%) is given in parentheses. Different letters indicate significant difference in the proportions between the measured species ($P < 0.05$).

Table 2: the mean aboveground net CO_2 exchange (NE_{above}), respiration (R_{above}), photosynthesis (P), root respiration in light (R_{root}^{light}) and darkness (R_{root}^{dark}), total respiration (R_{tot}), net primary production (NPP), transpiration (T) and water use efficiency (WUE) with standard error of the measured species

Species	Calvul	Pinsyl	Vacmyr	Vacvit
N	8	7	7	8
NE_{above} (nmol g^{-1}) s^{-1})	−2.41 ± 0.46 a	−6.27 ± 0.64 b	−2.72 ± 0.22 a	−2.88 ± 0.25 a
R_{above} (nmol g^{-1} s^{-1})	1.69 ± 0.12 a	3.34 ± 0.69 b	1.24 ± 0.24 a	1.65 ± 0.26 a
P (nmol g^{-1} s^{-1})	4.10 ± 0.55 a	9.61 ± 1.14 b	3.96 ± 0.24 a	4.53 ± 0.46 a
R_{root}^{dark} (nmol g^{-1} s^{-1})	0.73 ± 0.34 a	4.53 ± 0.96 b	0.41 ± 0.24 a	0.78 ± 0.24 a
R_{root}^{light} (nmol g^{-1} s^{-1})	1.27 ± 0.41 a	4.30 ± 0.92 b	0.69 ± 0.31 a	1.16 ± 0.26 a
R_{tot} (nmol g^{-1} s^{-1})	2.95 ± 0.31 a	7.75 ± 1.41 b	2.21 ± 0.24 a	2.81 ± 0.38 a
NPP (nmol g^{-1} s^{-1})	1.15 ± 0.47 a	1.86 ± 0.59 a	1.76 ± 0.20 a	1.73 ± 0.24 a
T (μmol g^{-1} s^{-1})	1.34 ± 0.21 a	2.56 ± 0.47 b	0.89 ± 0.10 a	1.44 ± 0.18 a
WUE (mmol mol^{-1})	3.28 ± 0.33 a	4.16 ± 0.42 a	4.67 ± 0.40 a	3.39 ± 0.40 a

All fluxes are normalized by total biomass. Different letters indicate significant difference in the fluxes between the measured species ($P < 0.05$).

The belowground CO_2 emissions (R_{root}^{dark} and R_{root}^{light}) of the dwarf shrubs were very low especially in dark conditions. The R_{root}^{dark} of the dwarf shrubs was ~10% to 20% of P whereas for Pinsyl, R_{root}^{dark} was ~46% of P (Table 2). The R_{root}^{light} of Pinsyl was of a similar magnitude than R_{root}^{dark}, but for dwarf shrubs, R_{root}^{light} was ~50% to 70% higher than that of R_{root}^{dark}. The difference between R_{root}^{dark} and R_{root}^{light} was significant with Vacvit (P = 0.016) and Calvul (P = 0.004), whereas it was not significant with Pinsyl (P = 0.201). Even if R_{root}^{light} of Vacmyr were in general higher than R_{root}^{dark}, the difference was not clearly significant (P = 0.066).

Pinsyl had the highest transpiration when normalized by total biomass (Table 2) but when normalized by leaf mass, Vacmyr had similar transpiration rates significantly differing from those of Vacvit and Calvul (see online supplementary Table S3). Vacmyr and Pinsyl had the highest WUE i.e. they lost the lowest amount of water per assimilated carbon but WUE values did not significantly differ between the species.

Stable isotopes

Stable isotope signatures were the most negative in leaves of the unlabeled dwarf shrubs and increased slightly in the stems, rhizomes and roots (see online supplementary Table S4). The differences were significant only with Vacmyr whose leaves had a lower signature than that of the other organs (app. −31.1 vs. −28.1‰, respectively). The unlabeled control soil without a plant had a $\delta^{13}C$ signature of −28.4 ‰ with a standard error of 0.06 ‰.

The relative distribution of the ^{13}C-label was the highest in leaves decreasing towards roots for all the dwarf shrubs whereas for Pinsyl, the highest share of ^{13}C was in the stem (Fig. 2). The distribution of $\delta^{13}C$ widely differed from the biomass fractions (Fig. 2, see online supplementary Fig. S1). The biggest differences were found in roots whose relative share of $\delta^{13}C$ was much lower than their relative biomass. Instead,

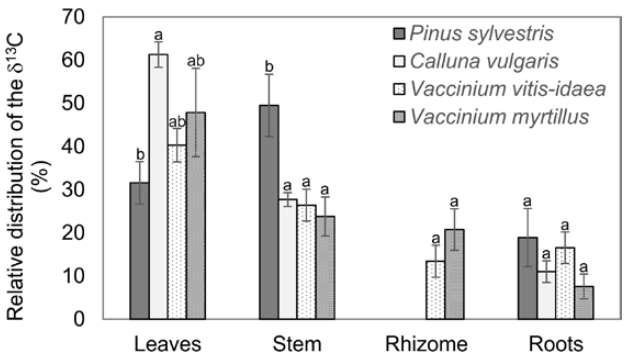

Figure 2: the relative distribution of assimilated ^{13}C in different seedling organs. Error bars represent standard error. Different letters indicate significant difference in the proportions between the measured species ($P < 0.05$).

more $\delta^{13}C$ was found aboveground compared with the biomass shares, especially in the stems of Pinsyl. In leaves, the biomass shares and $\delta^{13}C$ values were similar to one another except for Pinsyl whose share of $\delta^{13}C$ in leaves was decreased notably and for Vacmyr, whose share of $\delta^{13}C$ in leaves was more than double that of biomass. The share of $\delta^{13}C$ in the rhizome of Vacmyr was much higher than the share of biomass in contrast to Vacvit where the distribution of $\delta^{13}C$ in the rhizome and biomass were similar.

DISCUSSION

We determined the full carbon balance of the three most common ericoid dwarf shrub species from boreal Scots pine forests for the first time and compared them to *Pinus sylvestris*. We were able to detect significant differences in the C dynamics of these forest plant species using three different approaches. This knowledge will significantly improve

current understanding of CO_2 sources and sinks in boreal ecosystems.

Our results indicated that the growth rates of the studied dwarf shrub species are similar in the environmental conditions tested. Differences in seedling age and environmental conditions such as light availability, competition and soil nutrition were naturally reflected in the growth rate. For example, the growth rate of Scots pine would be greater in high light conditions as a pioneer species. However, the conditions we selected represent the common environmental conditions found on the forest floor in the southern boreal zone.

The long-term allocation rate was also surprisingly similar within the species tested. The mean shoot:root ratio of *C. vulgaris* (1.92) is very similar to that previously reported 1.97 for 1-year-old seedlings in Norway (Verburg *et al.* 1998). However, a value of 1.2 was reported for ~2-year-old seedlings (Meyer-Gruenefeldt *et al.* 2015). Nevertheless, our seedlings germinated from seeds and it is therefore difficult to compare biomass allocation in our study with that reported in earlier studies. Earlier field studies for *Vaccinium* species mostly fail to identify roots individually or species-specifically (Chapin and Shaver 1996; Gerdol *et al.* 2004; Grogan and Jonasson 2003).

Carbon allocation patterns of the different plant organs are known to vary throughout the life cycle of plants (Kozlowski 1992). The biomass of plants reflects long-term allocation of C. ^{13}C pulse labelling can be used to detect short-term C allocation. It was shown that at the age of the labelling (1.3–1.6 years), all species accumulate more carbon above ground than the distribution biomass amongst organs would suggest. The share of the label in roots was ~50% lower short-term assays than the overall share in biomass which indicates that in these conditions, all species measured first grow sufficient root biomass before greater allocation to aboveground parts. However, the share of rhizome in *Vaccinium* species increases as the plants age (Kaur *et al.* 2012) which is consistent with our study as an increased allocation of recently assimilated C to rhizome in *V. myrtillus*.

Compared with the dwarf shrubs, *P. sylvestris* seems to allocate most of recently assimilated C to the stem, which at this age is probably due to the plant's capacity to grow tall trunks. On the other hand, the lower relative share of the label in the leaves of Scots pine may indicate higher transport rate of assimilates compared to those of dwarf shrubs. Our sampling time was selected according to Pumpanen *et al.* (2009) to study and follow the relative share of the label within the plants. Nevertheless, it would have required a different experimental setup to see how much of the label was actually bind to biomass and how much the observed differences reflect the variation in transport rate and storage potential.

Pinus sylvestris clearly has the highest flux rates of all showing increased metabolism compared with ericoid plants. Remarkably, the increased metabolism did not result in significantly faster accumulated biomass or a higher NPP compared to ericoid plants as their carbon losses in autotrophic respiration were the highest. Scots pine appears to have a particularly rapid belowground activity caused by either roots or root-associated microflora. The reason for this might relate to its ectomycorrhizal fungi that can be more predominant and large in biomass than the ericoid mycorrhizal fungal association in dwarf shrubs. In this study, we did not follow the differences in these associations between the species studied but ericoid mycorrhiza do not typically form extensive hyphal networks in soil in contrast to many ectomycorrhizal species (Smith and Read, 2008). Vigorous fungi associated with pine would explain the generally high rate of metabolism that limited biomass accumulation. Ectomycorrhizal fungi are a great sink of carbon and for ericoid species; the lack of such strong sink might have down-regulated also photosynthetic activity (Paul and Foyer 2001). The higher CO_2 emissions resulting from higher C input belowground might also indicate that Scots pine has a higher priming effect on the decomposition of soil organic matter than the ericoid dwarf shrubs. Further studies are needed to determine whether the decomposition of organic matter in the microcosms containing Scots pine seedlings was higher than in those containing dwarf shrub seedlings.

Remarkably, the evergreen dwarf shrubs have lower root respiration in darkness than in light, i.e. when the shoot is photosynthesizing. Meanwhile, root respiration by Scots pine was independent of light conditions. The reason for this remains unclear but it might be that Scots pine has a better capacity to regulate internal carbon storages than dwarf shrubs allowing rather continuous C flow belowground despite the variation in photosynthesis. Another explanation, also related to the continuous belowground C flow, is that the constant activity of root-associated fungi may balance out differences in CO_2 output from the ectomycorrhizal roots in light and dark conditions. However, further studies including detailed microbial data are required to support these assumptions.

Many studies on grasslands or on similar short vegetation show minor time lags (0–4 h) between changes in GPP and soil respiration (e.g. Bahn *et al.* 2009; Han *et al.* 2014; Yan *et al.* 2011). Our results support these findings and suggest that in the short term, photosynthesis and maintenance respiration in Scots pine seem to be more independent of each other than in especially the evergreen dwarf shrubs. Nevertheless, some studies indicate that autotrophic respiration of trees also has a diurnal cycle (Kodama *et al.* 2008; Marron *et al.* 2009; Savage *et al.* 2013). A compilation of 47 studies concluded that the transfer of labelled C belowground takes a few days and that the rate of transfer differs between broadleaved and coniferous species decreasing with temperature and soil water content (Epron *et al.* 2012). Our results suggest that the relatively higher proportion of forest floor CO_2 emissions during the daytime originate from ground vegetation rather than trees compared with the night time fluxes due to the light-dependent nature of root respiration in evergreen dwarf shrubs.

Another possibility is the lack of light-related differences in the root respiration of Scots pine might lie in the high-transpiration rate. There is evidence that some of the respired

CO_2 is transported upwards to the stem during high transpiration (Bloemen *et al.* 2014; Grossiord *et al.* 2012). However, the difference in the biomass-based root respiration between Scots pine and dwarf shrubs was many folds higher than the difference in the transpiration rates indicating that the internal transport of CO_2 is not the most plausible cause of the observed differences in this study.

The transpiring plants may have decreased the soil moisture faster than the control soil and consequently caused differences in the heterotrophic respiration (Davidson *et al.* 1998; Skopp *et al.* 1990). The presence or absence of a plant also has a big impact on the microbial community composition in the soil as the root-associated microflora generally differs in composition from heterotrophic microbial communities (Buee *et al.* 2009). To estimate the proportion of heterotrophic (basal) respiration from autotrophic respiration in non-disturbed soils with plant roots is a challenge that needs further investigations with sophisticated methods (e.g. $^{13}CO_2$ or $^{14}CO_2$ labelling). Nevertheless, in our study, the species-specific differences are detectable despite a possible offset of heterotrophic respiration. Environmental conditions in the field fluctuate but our experimental design enabled a reliable partitioning of the fluxes by stabilizing the environment, most importantly the temperature.

CONCLUSIONS

Our results indicate that despite obvious differences for example in leaf morphology and in biomass allocation, young dwarf shrubs have similar rates of aboveground and belowground CO_2 exchange that differ significantly from those of Scots pine. The root-originated respiration rates of the dwarf shrubs differ greatly in light and dark conditions, whereas those of Scots pines appear to be independent of the aboveground photosynthesis. Although larger plants may have different carbon dynamics than the seedlings studied in this microcosms experiment, our results suggest that especially evergreen ericoid plants rapidly allocate assimilated C to belowground compartments and outside roots. Therefore, much of the soil CO_2 production detected in soil respiration measurements during light hours is likely to be derived from the activities of these plant species. In contrast, our data suggest that the nighttime soil respiration measurements may better reflect the contribution of the tree root-associated autotrophic respiration. The soil chambers commonly used in the field also include dwarf shrubs. Therefore, our data can be used to estimate the contribution of dwarf shrubs to soil CO_2 fluxes allowing a better prediction of the effects of environmental changes on the source and sink capabilities of boreal forest ecosystems.

SUPPLEMENTARY MATERIAL

Supplementary material is available at *Journal of Plant Ecology* online.

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